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DISPERSAL OF ZOOXANTHELLAE ON CORAL REEFS BY PREDATORS ON CNIDARIANS

GISÈLE MULLER PARKER*

Department of Biology, University of California, Los Angeles, California 90024

ABSTRACT

Fish and nudibranchs prey on cnidarians that contain high densities of symbiotic dinoflagellates (zooxanthellae). Several fish (*Arothron meleagris, Chaetodon auriga,* and *Chaetodon unimaculatus*) and one nudibranch (*Berghia major*) feed on the Hawaiian symbiotic sea anemone *Aiptasia pulchella.* Fecal material of these predators consisted primarily of zooxanthellae, which were shown to be photosynthetically active and capable of re-establishing symbioses with aposymbiotic *A. pulchella.*

INTRODUCTION

Symbiotic dinoflagellates (zooxanthellae = *Symbiodinium microadriaticum*) are major primary producers on coral reefs (Muscatine, 1980). They occur in high densities in corals and other cnidarian hosts but have yet to be found in abundance in the water column. Since zooxanthellae must be acquired *de novo* with each sexual generation in many symbioses (Trench, 1979), and since cnidarians show specificity for different strains of zooxanthellae (Schoenberg and Trench, 1980), the question often arises: how are zooxanthellae dispersed over coral reefs? There are several ways in which zooxanthellae are freed from animal tissue: by extrusion, either spontaneous (Steele, 1977) or as a result of osmotic (Goreau, 1964) or temperature (Buchsbaum, 1968) stress, or as a result of predation on the host. Motile stages also can arise from zooxanthellae in decaying host nudibranch tissues (Kempf, 1984). The potential significance of predator feces as an agent for the dispersal of viable zooxanthellae has not been previously reported.

Many predators on corals and other symbiotic cnidarians have been described. For example, fishes of the Marshall Islands include browsers on coral polyps (Families: Chaetodontidae, Monacanthidae), grazers on coral heads (F.: Chaetodontidae, Scaridae, Balistidae, Monacanthidae), and feeders on branching coral tips (F.: Balistidae, Monacanthidae, Tetraodontidae, Canthigasteridae) (Hiatt and Strasburg, 1960; see also Hobson, 1974; Randall, 1974). Robertson (1970) reviewed invertebrate feeders on corals, particularly gastropods. However, none of these authors considered whether zooxanthellae were digested by the predators. The liberation of zooxanthellae from host tissue has two important ecological consequences: zooxanthellae are dispersed and may reinfect other hosts, and they become available as a food source for herbivores.

The Hawaiian sea anemone *Aiptasia pulchella* is found in shallow (<2 m) reef areas and in protected lagoons. The puffer *Arothron meleagris,* two species of butterflyfish, *Chaetodon auriga* and *C. unimaculatus,* and the nudibranch *Berghia major* were found to feed on *A. pulchella.* As each sea anemone contained from 1.0 to 1.5 $\times 10^7$ zooxanthellae, or about 3.0×10^6 zooxanthellae per mg animal protein (Parker, in prep.), large numbers of zooxanthellae were consumed. This paper presents data which show that fecal pellets from these predators contained stages which were pho-

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* Current address: School of Life Sciences, University of Nebraska, Lincoln, Nebraska 68588.

tosynthetically active and gave rise to motile zooxanthellae. Fecal zooxanthellae were also capable of re-establishing symbioses with aposymbiotic *A. pulchella;* this indicates that predator feces may be important as a mode for the dispersal of symbionts and reinfection of symbiotic hosts.

Materials and Methods

Feeding experiments

Experiments with *Arothron meleagris* were conducted at the University of California, Los Angeles, using fish and *Aiptasia pulchella* collected in Hawaii. Those with butterflyfishes and nudibranchs were conducted at the Hawaii Institute of Marine Biology (HIMB), Coconut Island, Kaneohe Bay, Oahu, Hawaii, using freshly collected organisms. Butterflyfishes were collected on the reefs near HIMB with baited live traps. The nudibranch was found among populations of *A. pulchella* near the docks at HIMB.

In controlled experiments I allowed predators which had been starved for 24 hours to feed on sea anemones, then isolated them in tanks of clean sea water. Fecal material was collected with a pipette in some cases within minutes, but usually within several hours after defecation.

Photosynthetic ability of fecal zooxanthellae

The photosynthetic ability of fecal zooxanthellae from *Arothron meleagris* was tested by fixation of ^{14}C-bicarbonate. Feces were suspended in sea water, briefly homogenized with a glass tissue homogenizer, and filtered through coarse "nitex" screen to remove large clumps. The filtrate was centrifuged at $300 \times g$ in an IEC HN-S table centrifuge for two minutes to separate zooxanthellae from debris. The algal pellet was resuspended in filtered sea water, assayed for cell number, and diluted to a concentration of 2.90×10^5 zooxanthellae $\cdot$ ml^{-1}. Cells were incubated with $NaH^{14}CO_3$ (0.5 μCi $\cdot$ ml^{-1}) in duplicate test tubes at an irradiance of 100 μE $\cdot$ m^{-2} $\cdot$ s^{-1} at 25°C for one hour. Replicate tubes wrapped in foil were also incubated to correct for any heterotrophic fixation of ^{14}C-bicarbonate. Tubes were inverted every 15 minutes to resuspend settled cells.

Photosynthesis by fecal zooxanthellae was compared with that of freshly isolated zooxanthellae. The latter were obtained from sea anemones maintained in the dark for periods corresponding to the residence times of consumed zooxanthellae in fish guts. Zooxanthellae were isolated as follows. Sea anemones were homogenized using a glass tissue homogenizer. The homogenate was centrifuged at $550 \times g$ to separate animal and algal fractions and the resulting algal pellet was washed in filtered sea water several times. Final suspensions were diluted to the same cell concentration used for fecal zooxanthellae, and cells were incubated with ^{14}C-bicarbonate under the same conditions used for the fecal zooxanthellae and at the same time. At the end of the incubations, tubes of fecal and freshly isolated zooxanthellae were centrifuged at $550 \times g$, and the resulting algal pellets were rinsed three times in filtered sea water. The supernatant and final algal volumes were recorded, and three replicate 100 μl aliquots were taken from each fraction for liquid scintillation counting. The aliquots were acidified with an equal volume of 1 *N* HCl and placed under a heat lamp for three hours to drive off inorganic $^{14}CO_2$, then neutralized by addition of 1 *N* NaOH. Scintillation fluor (10 ml) was added and samples were counted on a Beckman LS 100C scintillation counter. CPM were converted to DPM by the external standard ratio method.

Reinfection experiments with aposymbiotic A. pulchella

To determine if fecal zooxanthellae from all four predators could re-establish symbioses with aposymbiotic sea anemones, two containers of aposymbiotic *A. pulchella* (with four sea anemones per container) were set up for each source of feces. Feces were added directly to one container. The other container served as a control for spontaneous reinfection. Both containers in each of the four sets were aerated and sea anemones were maintained under the same irradiance and fed every other day with freshly hatched *Artemia* nauplii. After four days the sea water was changed in both containers and feces were removed from the experimental container. Containers were then rinsed with fresh sea water every two days. One or two tentacles were removed every two days from all sea anemones, squashed, and examined microscopically for the presence of zooxanthellae. The number of zooxanthellae and the day of first appearance were recorded.

To determine the extent of reinfection after a long period of time, the photosynthetic abilities of experimental and control sea anemones were compared after 50 days by measuring oxygen flux and fixation of ^{14}C-bicarbonate. Oxygen flux measurements were made in a rectangular plexiglas chamber (volume: 49.5 ml) with a Clark YSI 4004 oxygen electrode connected to a chart recorder. The chamber was surrounded by a water jacket maintained at 25°C. Irradiance sufficient for light-saturated photosynthesis by zooxanthellae in these sea anemones, 2000 $\mu E \cdot m^{-2} \cdot s^{-1}$, was provided by a 250 watt tungsten-halogen lamp. Several measurements in the light and dark were made for each sea anemone. Sea anemones were then incubated with 0.25 μCi $NaH^{14}CO_3$ per ml for one hour at 2000 $\mu E \cdot m^{-2} \cdot s^{-1}$ irradiance and 25°C. At the end of the incubations they were rinsed in non-radioactive sea water, homogenized, and the homogenate sampled for liquid scintillation counting, zooxanthellae cell numbers, and total protein. Aliquots for liquid scintillation counting were treated as previously described. To determine the density of zooxanthellae in experimental and control sea anemones, the homogenates were centrifuged to separate animal and algal fractions and the resulting algal pellet was washed three times with filtered sea water. Cell counts were made on the final algal suspensions. Supernatants were combined and aliquots analyzed for animal protein. Protein analysis was done by the method of Lowry *et al.* (1951). The density of zooxanthellae was expressed as numbers of zooxanthellae per mg animal protein.

Statistics

To determine whether the results of the reinfection experiments were significantly different for control and experimental groups of sea anemones, I used the Mann-Whitney U test (Sokal and Rohlf, 1969). Nonparametric statistics were necessary as data sets were found to be heteroscedastic (F_{max}-test; Sokal and Rohlf, 1969).

Results

Feeding experiments

A. pulchella was fed to puffers (*Arothron meleagris*) previously maintained on fresh mussel meat and occasionally sea anemones. Puffers curled back their lips and used their fused beak-like teeth to chop off the crown of tentacles from individual sea anemones. After the tentacles were consumed the puffer would eat the rest of the body column before proceeding to the next sea anemone. A puffer ate 15 to 45 sea anemones at one feeding. Defecation of sea anemone remains occurred 12 to 46 hours afterwards.

Individuals of *A. pulchella* from natural populations living on dead coral skeletons and rocks were offered to many different reef fishes in Hawaii. The butterflyfishes *Chaetodon auriga* and *C. unimaculatus* readily ate these sea anemones, with each fish consuming about five sea anemones at one feeding. The tentacle crowns and upper parts of the body column of sea anemones were preferred, and defecation occurred within 12 to 24 hours after feeding.

The nudibranch *Berghia major* was found in association with natural populations of *A. pulchella* in Hawaii. It may be that *A. pulchella* is a significant prey item for *B. major,* as nudibranchs laid egg strings close to these sea anemones. The nudibranch limited its feeding to sea anemone tentacles. One nudibranch consumed the tentacles of three sea anemones (approx. 120 tentacles) daily. Tentacles were clipped off near the oral disk. Nudibranchs defecated within 24 hours after feeding. *B. major* differs from the fish in that it stores zooxanthellae and nematocysts in its cerata. Zooxanthellae stored in the cerata are presumed to be photosynthetically active to some extent, as nudibranchs consumed less oxygen in the light than in the dark (Parker, unpubl.).

Fecal material from the three predatory fish and the nudibranch consisted mostly of zooxanthellae. Light microscopic examination of feces showed that fecal zooxanthellae appeared intact and that many of the cells were in the process of dividing (Fig. 1). Motile zooxanthellae arose within a few hours from defecated zooxanthellae when feces were placed under bright light.

Photosynthetic ability of fecal zooxanthellae

Photosynthetic rates of fecal zooxanthellae from the puffer *A. meleagris* are shown in Table I. Assimilation numbers, corrected for dark heterotrophic fixation, of fecal zooxanthellae are similar to those obtained for the freshly isolated zooxanthellae.

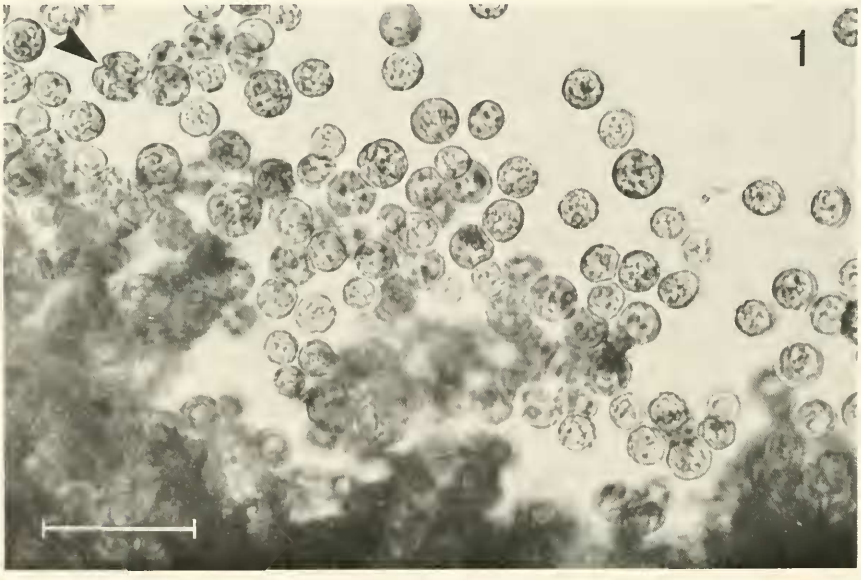

FIGURE 1. Light microscopic preparation of a fecal pellet from the nudibranch *Berghia major* which fed on the sea anemone *Aiptasia pulchella.* Arrow points to a dividing zooxanthella cell. Scale bar = 35 μm.

TABLE I

Assimilation numbers for zooxanthellae from Arothron meleagris *feces and freshly isolated from* Aiptasia pulchella

	Fecal zooxanthellae		Freshly isolated zooxanthellae	
Sample	Time in fish gut (hours)	Assimilation number* (mg C · h^{-1} · zoox. $cell^{-1}$) ($\times 10^{-9}$)	Time sea anemones kept in dark (hours)	Assimilation number (mg C · h^{-1} · zoox. $cell^{-1}$) ($\times 10^{-9}$)
A†	12–24	3.30	0	2.32
A	24–36	0.02	36	0.77
B	24–36	2.65	46	1.55
C	46	0.94		

* Assimilation number $= \left[\left(\frac{\text{light } ^{14}C \text{ fixation} - \text{dark } ^{14}C \text{ fixation}}{\text{added activity}}\right) \cdot \left(\frac{0.09 \text{ mg } CO_2}{\text{ml}}\right) \cdot \left(\frac{\text{total volume}}{\text{incubation}}\right) \cdot \left(\frac{12C}{44\ CO_2}\right) \cdot h^{-1} \cdot (\text{total number of zooxanthellae})^{-1}\right]$

$= \text{mg C} \cdot \text{zooxanthella cell}^{-1} \cdot h^{-1}$.

† Letters refer to different fish individuals used.

These results indicate that fecal zooxanthellae are photosynthetically active after passage through the predator's gut.

Reinfection experiments with aposymbiotic A. pulchella

Within six to ten days after the initial addition of feces to containers of aposymbiotic *A. pulchella,* zooxanthellae, including some in division stages, appeared in all experimental sea anemone tentacles. Fecal zooxanthellae from all four predators reinfected aposymbiotic sea anemones. Control sea anemone tentacles remained initially free of zooxanthellae, although some contained zooxanthellae after 50 days in the light.

To determine the extent of reinfection after a long period of time, experimental and control sea anemones were compared at 50 days. The data in Table II show that after 50 days experimental sea anemones contained high densities of zooxanthellae. Significantly fewer zooxanthellae per mg animal protein were found in control sea anemones than in experimental ones which had been exposed to predator feces [Mann-Whitney U test: $U_s = 16$, $P < .05$ (for *C. unimaculatus* experiment) $U_s = 12$, $P < .10$ (for *B. major* experiment)].

The photosynthetic performance of control and experimental sea anemones after 50 days was evaluated from ^{14}C-bicarbonate fixation and oxygen production and consumption data (Table III). Significantly more carbon (DPM · mg sea anemone $protein^{-1}$) was fixed in experimental sea anemones than in control sea anemones [Mann-Whitney U test: $U_s = 16$, $P < .05$ (for *C. uminaculatus* experiment) $U_s = 12$, $P < .10$ (for *B. major* experiment)]. Experimental sea anemones showed net oxygen production in the light whereas control sea anemones consumed oxygen under the same conditions. Rates of oxygen consumption in the dark for both groups are included for comparison.

In separate experiments, fecal pellets were placed onto the oral disks of sea anemones to determine whether these were ingested. In most trials, feces were readily ingested and retained by both symbiotic and aposymbiotic sea anemones.

TABLE II

Zooxanthellae in experimental and control sea anemones 50 days after initial challenge

Donor predator (source of feces)	Recipient sea anemones	Total number of zooxanthellae per sea anemone ($\times 10^6$)	Number of zooxanthellae per mg animal protein ($\times 10^6$)
Chaetodon unimaculatus	Experimental (+ feces)	5.78 (±.28)† n = 4	2.88 (±.33) n = 4
	Control	0.08 (±.04) n = 4	0.05 (±.02) n = 4
Berghia major	Experimental (+ feces)	8.76 (±.78) n = 3	2.70 (±.02) n = 3
	Control	1.09* (±.84) n = 4	0.50 (±.38) n = 4

* One control sea anemone became densely packed with zooxanthellae. If it is excluded the mean number of zooxanthellae per sea anemone is 0.268×10^6.

† ±S.E.

DISCUSSION

Many symbiotic associations rely on a renewed establishment of the symbiosis after sexual reproduction (Trench, 1979). A few examples include the gorgonian *Pseudopterogorgia bipinnata* (Kinzie, 1974), the coral *Astrangia danae* (Szmant-Froelich *et al.*, 1980), the sea anemones *Anthopleura elegantissima* and *A. xanthogrammica* (Siebert, 1974), and the clam *Tridacna squamosa* (Fitt and Trench, 1981). The eggs and planula larvae of *Aiptasia pulchella* do not contain zooxanthellae (Parker, unpubl. obs.). As symbionts must be obtained from the environment, predator feces may be an important source of zooxanthellae for reinfection.

TABLE III

Productivity in experimental and control sea anemones 50 days after initial challenge

Donor predator (source of feces)	Recipient sea anemones	^{14}C fixed†	O_2 produced (+) or consumed (−)*	
			Light ($\times 10^{-2}$)	Dark ($\times 10^{-2}$)
Chaetodon unimaculatus	Experimental (+ feces)	53,302 (±8568)†† n = 4	+2.381 (±.538) n = 4	−1.003 (±.159) n = 4
	Control	2126 (±1057) n = 4	−0.411 (±.067) n = 3	−0.434 (±.143) n = 3
Berghia major	Experimental (+ feces)	131,600 (±33,533) n = 3	+2.327 (±.288) n = 3	−0.779 (±.221) n = 3
	Control	16,119 (±12,863) n = 4	−0.140 (±.253) n = 4	−0.809 (±.202) n = 4

* $(mg\ O_2) \cdot (mg\ sea\ anemone\ protein)^{-1} \cdot h^{-1}$.

† $DPM \cdot (mg\ sea\ anemone\ protein)^{-1}$.

†† ±S.E.

Although zooxanthellae are believed to be a single species, some strain specificity has been demonstrated in certain hosts (Schoenberg and Trench, 1980). Kinzie and Chee (1979) showed that aposymbiotic *A. pulchella* reinfected with zooxanthellae isolated from different hosts had different growth rates; sea anemones reinfected with zooxanthellae from *A. pulchella* and the scyphozoan *Cassiopea xamachana* grew as well as normal *A. pulchella* whereas those infected with zooxanthellae isolated from the gastropod *Melibe pilosa* and the clam *Tridacna maxima* grew no better than control aposymbiotic sea anemones. Therefore mechanisms which increase zooxanthellae dispersal, and thus contribute to the probability of host contact with the "correct" strain, are important. Mobile predators such as reef fish which release viable zooxanthellae in their feces may be significant in the dispersal of zooxanthellae over long distances.

Aposymbiotic sea anemones which had been exposed to feces contained high densities of zooxanthellae after 50 days (Table II). These densities were similar to those of symbiotic *A. pulchella,* which have algal densities ranging from 1.5 to 3×10^6 zooxanthellae per mg animal protein (Parker, in prep.). Although sea anemones exposed to fecal zooxanthellae had significantly more zooxanthellae, some of the control sea anemones became repopulated with zooxanthellae. Zooxanthellae in control sea anemones were probably residual cells, occasionally found in aposymbiotic *A. pulchella,* which multiplied under the favorable culture conditions.

Predation on symbiotic cnidarians may increase the chances of zooxanthellae coming into contact with other host organisms, as fecal pellets were found to be readily ingested by *A. pulchella.* Feces contain varying quantities of semi-digested animal remains which may stimulate ingestion in potential host organisms. It is not yet known if motile zooxanthellae released from the fecal material, direct ingestion of feces, or both processes, are responsible for reinfection of aposymbiotic hosts. Observations with cultured zooxanthellae indicate that the motile forms are more readily ingested by potential hosts than the non-motile zooxanthellae (Kinzie, 1974; Fitt and Trench, 1981), but predator feces consist of freshly isolated zooxanthellae associated with animal remains and hence may not be directly compared with cultured zooxanthellae. It is likely that both motile zooxanthellae from fecal pellets and direct ingestion of fecal pellets are modes for acquisition of symbionts.

Many zooxanthellae in the process of cell division were found in predator feces (Fig. 1). It is possible that passage through the predator gut may expose zooxanthellae to higher nutrient levels than are found in sea water. This may actually stimulate growth and the survival of fecal zooxanthellae, as has been shown for algae in the guts of freshwater *Daphnia magna* (Porter, 1976).

This study shows that zooxanthellae defecated by some predators on cnidarians are viable. The different assimilation numbers for fecal and freshly isolated zooxanthellae cannot be directly attributed to factors such as residence time in the fishes or dark preconditioning of host sea anemones (Table I). Variability in the photosynthetic performance of fecal zooxanthellae may result from differences in the physiological environment encountered by zooxanthellae during passage through the fish guts. There is a possibility that some of the consumed zooxanthellae were digested. Herbivorous reef fishes may break down plant material by mechanical grinding or lysis by gastric acidity (Lobel, 1981). All zooxanthellae in the feces appeared intact and healthy (for example, Fig. 1), suggesting that mechanical breakdown is negligible. Harmelin-Vivien and Bouchon-Navaro (1983) studied the diets of butterflyfishes in Moorea. They measured the ratio of the weight of the alimentary tract to the weight of the fish (defined as a repletion index) and found that diet was correlated to the repletion index. They found that chaetodontids feeding primarily on corals had a

greater proportion of their body weight as alimentary tract, and from this concluded that corals represent more of a vegetable food (*i.e.,* zooxanthellae) than an animal food for butterflyfishes. However, they did not examine the fecal material of these butterflyfishes, nor did they present any physiological evidence for this conclusion. Although some herbivorous reef fishes have acidic gastric fluids and plant material is degraded by these (Lobel, 1981), no data on the acidity of gastric fluids of butterflyfishes and puffers are available. There is no information on cellulase activity in the butterflyfishes and puffer used in this study, however two species of estuarine puffers from Georgia showed no cellulase activity (Stickney and Shumway, 1974). The results of this study indicate that at least a significant proportion of consumed zooxanthellae are not digested by the butterflyfishes and puffers.

The nudibranch differs from the fish in that zooxanthellae are selected and stored in the cerata. Since these were photosynthetically active in the nudibranch, zooxanthellae must have a process whereby digestion in *B. major* is avoided. It has been suggested that the nutritional status of nudibranchs may influence the relative proportion of degenerate and healthy zooxanthellae in fecal material (Kempf, 1984).

Fish feces have been shown to be a food source for other reef fish (Robertson, 1982), but the importance of zooxanthellae released from feces as a food source for coral reef filter-feeding herbivores is unknown. Large numbers of zooxanthellae are released in predator feces. As an example, a puffer weighing 270 g wet weight readily consumes 30 sea anemones at one feeding. One feeding may thus liberate up to 330 million zooxanthellae. The relative contribution of fecal zooxanthellae to reef food sources will depend on the density of predators and the amount of symbiotic tissue consumed and assimilated. Zooxanthellae in fish feces may be an important source of energy for the reef community as well as a source of zooxanthellae for the reinfection of nonsymbiotic larvae and juveniles of host species.

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